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A New Middle Devonian Arthrodire (Placoderm Fish) from the Broken River Area, Queensland

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ABSTRACT. Associated bones of the trunk-armour belonging to a large brachythoracid arthrodire are described as *Confractamnis johnjelli* n.gen. and n.sp. The specimen comes from strata of probable Eifelian age in the Broken River Group of Queensland. It shows a range of derived brachythoracid features including reduction of dermal ornament, and strong development of the dermal neck joint articulation. The posterior dorsolateral and posterior lateral plates of the trunk armour were high and narrow, and the anterior lateral plate had a distinctive narrow bilobed dorsal angle as indicated by the shape of its overlap area on the anterior dorsolateral plate. A provisional reconstruction suggests that the bones came from a large fish over 2 m in length. A cross section of the trunk armour is compared with the large arthrodire *Taemasosteus* from the Early Devonian of Burrinjuck, New South Wales. A possible close relative of this new taxon has been illustrated from the Early Devonian of Morocco, supporting other indications of resemblance in placoderm fish assemblages between these regions of east and north Gondwana during the Early-Middle Devonian.

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Over 20 years ago Professor J.S. Jell (University of Queensland) made a small collection of limestone samples apparently containing bones from several localities in the Devonian outcrops of the Broken River area of Queensland (Fig. 1). They were sent to Professor K.S.W. Campbell (Australian National University), who passed on remains of placoderms (Devonian armoured fishes) to the author for preparation and study.

Acetic acid preparation, which completely removes bones (calcium phosphate) from limestone (calcium carbonate), revealed a small collection of six placoderm specimens from the ten original samples. Two samples belonged to one specimen (ANU V1028, described below). Three other samples contained only vertebrate microfossils (small scales and plates), which have been well documented from many horizons in the Broken River Devonian sequence by other authors (e.g., De Pomeroy, 1995, 1996; Turner *et al.*, 2000). The six placoderm specimens belong to two orders, the Antiarchi and the Arthrodira, which were the most successful of some seven orders within the class Placodermi (Denison, 1978; Young, 1986; Goujet & Young, 1995). The two antiarch specimens from Broken River were the best preserved, with articulated armours and some small bones of the jaws, cheek, and sclerotic ring surrounding the eye, not previously well documented for the group. They were described as two new genera (*Nawagiaspis* and *Wurungulepis*) by Young (1990).

The other four specimens can be assigned to the Arthrodira, by far the most diverse placoderm order, with its major subgroup, the Brachythoraci, comprising nearly 60% of about 170 genera within the Arthrodira (Carr, 1995). These specimens are much more fragmentary, probably because they belonged to considerably larger fishes, all representatives of the

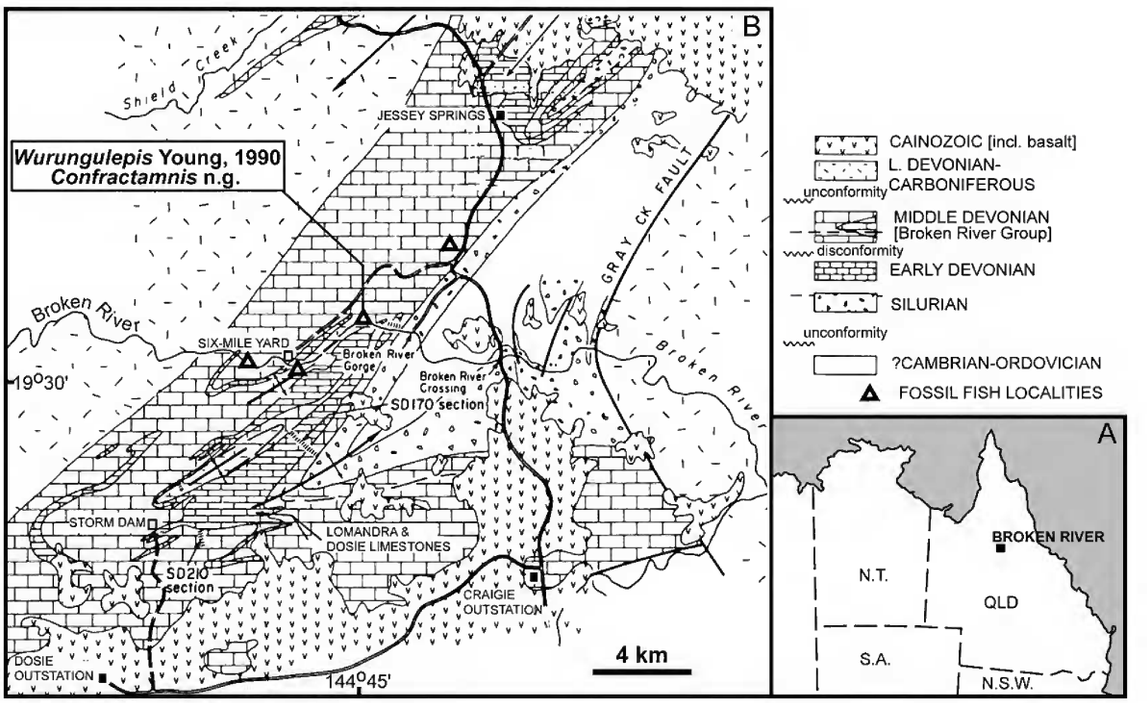

Fig. 1. (*A*) Location of the Broken River area in Queensland, Australia. (*B*) Geological map of the collecting area (modified from Turner *et al.*, 2000: fig. 2), showing the locality (Grid Reference 640 460) for the specimens described in this paper.

brachythoracid arthrodires. In marine environments of the Late Devonian the brachythoracids included probably the largest predators of their time (Young, 2003c).

The major radiation of brachythoracid subgroups had apparently already occurred by the Middle Devonian, and the diverse faunas that occupied shallow marine environments of eastern Australia during the Early-Middle Devonian have revealed primitive representatives that are important in resolving the origins and interrelationships of major brachythoracid subgroups (e.g., Lelièvre, 1995; Mark-Kurik & Young, 2003; Young *et al.*, 2001; Young, 2004a).

Two other brachythoracid specimens from the Broken River Devonian sequence have recently been described: a new species of the genus *Atlantidosteus* Lelièvre, 1984a, a large brachythoracid first recorded from the Early Devonian of Morocco (Young, 2003a), and a new genus and species *Doseyosteus talenti* Young, 2004b. The two specimens documented in this paper are the last to be described from the original J.S. Jell collection. An isolated suborbital plate of another arthrodire was illustrated by Turner *et al.* (2000: fig. 8.7), and an isolated toothplate was ascribed to ?*Ptyctodus* sp. (placoderm order Ptyctodontida) by Turner & Cook (1997). Other vertebrate macro-remains documented from the Broken River Devonian sequence include a lungfish skull (S. Turner, pers. comm.) and jaw remains of an onychodontid (Turner *et al.*, 2000: fig. 6). Apart from these osteichthyan (bony fish) remains, placoderm bones, mainly from brachythoracid arthrodires, seem to be most common amongst unprepared vertebrate samples from Broken River (S. Turner, pers. comm.).

Locality and age of the samples

The stratigraphic occurrence of various placoderm remains in the Broken River sequence was documented by Young (1993, 1996), De Pomeroy (1995, 1996), and Turner *et al.* (2000). Dating the sedimentary sequence is based mainly on conodonts (Mawson & Talent, 1989; Sloan *et al.*, 1995). Locality and age information for all previously described placoderm taxa from the original J.S. Jell collection was reviewed by Young (2004b), to clarify conflicting information previously published.

The specimens described below were sent to Canberra as three samples, two with the field number 58/L1 (ANU V1028), and one labelled 58/L2 (ANU V1031). According to information provided by J.S. Jell (letter of 17 April, 1980), they both came from University of Queensland locality L4399, north bank of the Broken River, Grid Reference 640 460 on the Burges 1:100 000 sheet (see Fig. 1). He suggested a Middle Devonian (?Eifelian) age for this locality. On the map of the area published by Sloan *et al.* (1995: fig. 2) the locality lies within the outcrop referred to as "undifferentiated Broken River Group".

The antiarch *Wurungulepis denisoni* Young, 1990 came from the same locality (erroneously given as L4339 by Young, 1990: 45). On this evidence, a "*Wurungulepis-Atlantidosteus* fauna", of assumed Eifelian age, was listed in the macrovertebrate zonation of Young (1993, 1996). However De Pomeroy (1995: 480) assigned *Wurungulepis* an older age—the late Emsian *serotinus* Conodont Zone—citing a personal communication of J.A. Talent. This information was repeated by Turner *et al.* (2000: 498).

No conodont data were obtained during acid preparation of the specimens described below, so their precise position relative to the standard conodont zonation is uncertain. Young (2004b) concluded that the original age assessment of Eifelian for the antiarch *Wurungulepis*, from the same locality, was most consistent with current knowledge of the stratigraphic distributions of the Antiarchi, a large and diverse group comprising some 45 named genera and 154 species. Various advanced features of the brachythoracid arthrodire described below are consistent with this interpretation.

Abbreviations

Repositories for material are indicated by specimen prefixes as follows: **ANU V**, Department of Earth and Marine Sciences, Australian National University, Canberra; **MCD**, Moroccan specimens in Muséum national d'Histoire naturelle, Paris.

Standard abbreviations for placoderm dermal bones are used in the text and figures, with bone overlap areas designated as "contact face" (*cf*) on the inner surface, or "overlap area" (*oa*) on the outer surface. These and other anatomical abbreviations used in the figures are as follows: *ADL*, anterior dorsolateral plate; *AL*, anterior lateral plate; *cd*, glenoid condyle of dermal neck-joint; *cf.ADL*, area overlapping ADL plate; *cf.PDL*, area overlapping PDL plate; *cf.PL*, area overlapping PL plate; *dla*, dorsolateral axis separating dorsal and lateral walls of the trunk armour; *fo.PL*, fossa on PDL plate receiving dorsal corner of PL plate; *gr.AL*, anterior groove for AL plate; *IL*, interolateral plate; *laf*, articular fossa for dermal neck-joint; *llc*, main lateral line sensory canal; *MD*, median dorsal plate; *oa.ADL*, area overlapped by ADL plate; *oa.AL*, area overlapped by AL plate; *oa.MD*, area overlapped by MD plate; *oa.PDL*, area inserting into fossa of PDL plate; *o.PDL*, area of PDL plate overlapped by ADL; *o.PL*, area of PL plate overlapped by ADL plate; *pap*, para-articular process; *PDL*, posterior dorsolateral plate; *PL*, posterior lateral plate; *pr.sg*, subglenoid process; *ri.cd*, ridge crossing inner surface of articular condyle; *ri.p*, posterior ridge; *ri.vt*, vertical ridge; *SP*, spinal plate; *th*, thickening; *vg*, vascular grooves; *vs.cd*, ventral surface of articular condyle.

Systematic palaeontology

Class Placodermi McCoy, 1848

Order Arthrodira Woodward, 1891

Suborder Brachythoraci Gross, 1932

Confractamnis johnjelli n.gen. and n.sp.

1992 eubrachythoracid nov.–Young *et al.*, 1993: 247 (*pars*).

Name. From the Latin *confractus* (broken) and *amnis* (stream or river), with reference to the Broken River. The species name recognizes the collector, Prof. John Jell, University of Queensland, who has conducted research in the Devonian of the Broken River area over many decades.

Diagnosis. A large brachythoracid attaining a length of at least 2 m; trunk armour high, with anterior lateral, posterior dorsolateral, and posterior lateral plates all dorsoventrally elongated. Median dorsal plate enclosing a midline angle of about 150° between left and right laminae. Anterior dorsolateral plate crossed by single sensory canal groove close and subparallel to the lateral margin of the median dorsal plate. Dorsal corner of anterior lateral plate narrow, rounded, and bilobed, with 25–30° angle between main margins. Posterior dorsolateral plate extensively overlapped by anterior dorsolateral plate; posterior lateral plate with high and narrow exposed part, and elongate anterior overlap for the anterior dorsolateral plate. External surface of dermal bones smooth, or with very fine, closely spaced tuberculation of low relief.

Remarks. Because the skull roof is unknown in this new taxon, only trunk armour characters are available for assessing its affinities. It is clearly not a coccosteid, in which the ADL plate is crossed by an additional ventral sensory canal groove. The absence of the ventral sensory groove is one of four characters by which Carr (1991: 382) characterized the most derived pachyosteomorph subgroup within the Brachythoraci (comprising the Dinichthyidae and Aspinothoracidi). Within the former family, *Eastmanosteus* differs from the new taxon in possessing tubercular ornament, and both *Eastmanosteus* and *Dunkleosteus* have an extensive exposed part of the ADL plate above the sensory groove. *Levisosteus* Otto, 1999 is a poorly known brachythoracid showing possible affinity with *Dunkleosteus*, and indicating that ornament reduction may have occurred by the Eifelian, but its trunk armour is completely unknown, so no other comparisons are possible with the specimens described here. The aspinothoracids are characterized by various skull features in addition to the absence of a spinal plate in the trunk armour (Carr, 1991). There is no information on whether this small bone was present in *Confractamnis* n.gen., but it is likely that the spinal was lost independently in several groups, as suggested by Denison (1984). One group in which this had occurred by the Middle Devonian is the Heterostiidae. *Heterostius* resembles *Confractamnis* n.gen. in large size, reduction of ornament, and position of the lateral line groove near the dorsal exposed edge of the ADL plate. *Heterostius*, however, differs in extreme trunk armour reduction, with the AL plate fused to the ADL plate, whereas the AL was clearly a separate bone in *Confractamnis* n.gen. The Emsian forms *Tityosteus, Taemasosteus* and *Antineosteus* also resemble *Confractamnis* n.gen. in the dorsal position of the sensory groove on the ADL plate, but differ in the dorsal configuration of the AL plate (as indicated by the shape of its overlap on the ADL), in the shape of the PDL and PL plates, in the much flatter MD plate (*Tityosteus* and *Antineosteus*), and in the transversely elongate articular condyle attached along its length to the ADL plate (*Antineosteus*; a character defining the Homostiidae). Close affinity with *Atlantidosteus* (known from two species, one in Morocco and one in the Broken River sequence) can be excluded on the assumption that this taxon was a homostiid, with a dorsoventrally compressed trunk armour. One isolated ADL plate from the Emsian of Morocco resembles *Confractamnis* n.gen. in its pointed articular condyle, the narrow rounded dorsal angle of the overlap area for the AL plate, and the position of the sensory groove close and subparallel to the lateral margin of the MD. This specimen may represent a closely related taxon, but it differs from *Confractamnis* n.gen. in its smaller size, coarse tubercular ornament, more acute angle between the dorsal lamina of the ADL plate and the long (transverse) axis of the articular condyle, and the lack of a bilobed dorsal corner on the AL plate.

Material. ANU V1028 (holotype), a large left ADL plate with part of the MD plate attached, associated with left PDL and PL plates (all incomplete); ANU V1031, a very incomplete MD plate.

Locality. University of Queensland locality L4399, north bank of the Broken River, Grid Reference 640 460 on the Burges 1:100 000 sheet (see Fig. 1); field numbers 58/L1 (V1028) and 58/L2 (V1031).

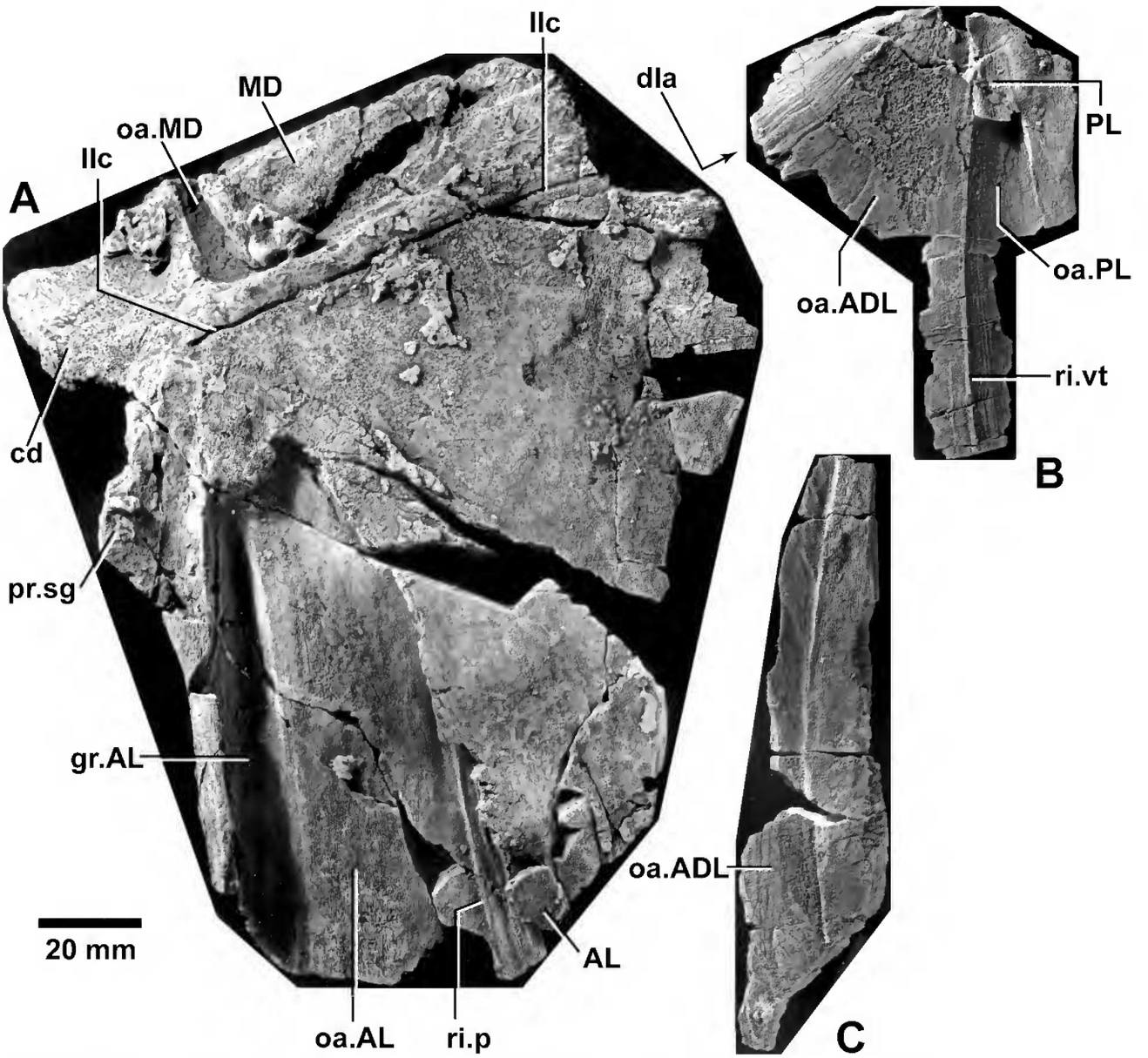

Fig. 2. *Confractamnis johnjelli* n.gen. and n.sp. ANU V1028 (holotype). Bones of the trunk armour in external view (all incomplete). (*A*) Left ADL plate, with part of the MD plate and a fragment of the AL plate attached; (*B*) left PDL plate, with part of the PL plate attached; (*C*) left PL plate. All specimens acid-prepared, and whitened with ammonium chloride for photography.

Horizon and age. According to information provided by Prof. J.A. Talent to A. Basden (pers. comm., 28 August 1995), the holotype of *Wurungulepis*, from the same locality as the material described here, came from strata that were pre-Dosey Limestone in the sequence, and equivalent to the Bracteata Formation and Lomandra Limestone. Outcrop in this vicinity is referred to as "undifferentiated Broken River Group" on the most recent published geological map (Sloan *et al.*, 1995: fig. 2). Prof. J.S. Jell (letter of 17 April, 1980) suggested a Middle Devonian (?Eifelian) age for this locality, and the sequence is shown spanning the Emsian-Eifelian boundary by Sloan *et al.* (1995: fig. 3).

Description. The holotype (ANU V1028) includes remains of four bones from the trunk armour of a very large brachythoracid. The left anterior dorsolateral (ADL) plate is particularly massive (Figs. 2A, 3), with the bone some 35 mm thick at the base of the articular condyle (cd) for the dermal neck-joint. The ventral part of the ADL is missing, and the posterior margin is broken and incomplete, but the fragmented posterior parts reduce in thickness to a little more than 1 mm, with part of the actual margin preserved. Together with the evidence of adjacent bones it is possible to determine the general shape of the ADL plate, except for the extent of the ventral margin.

The external surface of the ADL (Fig. 2A) shows two deeply incised overlap areas for the median dorsal (MD) and anterior lateral (AL) plates (oa.MD, oa.AL). A broken fragment of the left anterolateral corner of the MD plate is still attached to the specimen, but slightly displaced. Its thickness (13 mm), so close to the lateral margin, gives some indication of the large size of this bone (cf. ANU V1031 below). The rest of this normally massive bone was either weathered away, or perhaps was contained in another uncollected limestone block. The external surface of the MD fragment appears smooth, as does the exposed surface of the ADL. On close examination, some parts show a faint tuberculation of closely spaced fine tubercles (about 15 per

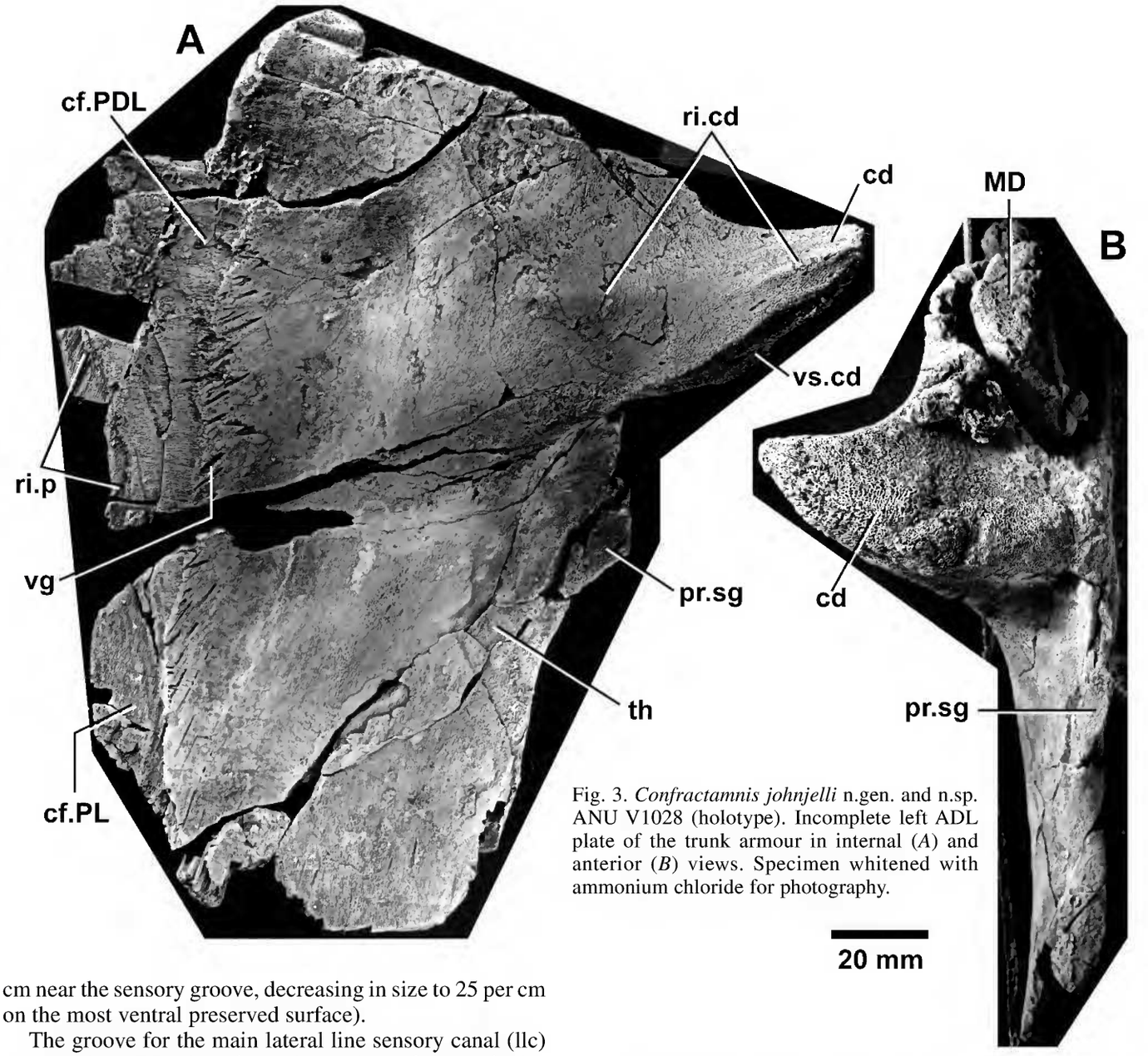

Fig. 3. *Confractamnis johnjelli* n.gen. and n.sp. ANU V1028 (holotype). Incomplete left ADL plate of the trunk armour in internal (*A*) and anterior (*B*) views. Specimen whitened with ammonium chloride for photography.

cm near the sensory groove, decreasing in size to 25 per cm on the most ventral preserved surface).

The groove for the main lateral line sensory canal (llc) crosses the ADL plate from the region of the articular condyle, as in all arthrodires with a developed dermal neck-joint. It runs, however, close and subparallel to the edge of the overlap for the MD, which is a point of difference to many other brachythoracids. The overlap area for the AL plate is set in about 10 mm along a deep anterior groove, which braced the AL against the anterior edge of the ADL plate (gr.AL, Fig. 2A). The overlap shows that the AL had a narrow rounded bilobed dorsal corner, which forms a much more acute angle (about 25–30°), and is quite different in shape to the triangular overlap of *Eastmanosteus* or *Dunkleosteus* (dorsal angle 45–50°). Near the ventral preserved edge the overlap area expands as a posterior embayment, in which a fragment of the overlying AL plate is preserved (AL, Fig. 2A). At its margin, this embayment slopes gradually to the external surface, in contrast to the thick and undercut margins of the deeply incised main part of the overlap area (oa.AL). These show that immediately dorsal to the embayment the posterior edge of the AL was enclosed by the ADL to a depth of about 6 mm. The undercut surface is exposed by the broken margin of the overlap area, to reveal a strong ridge (ri.p, Fig. 2A).

The articular condyle for the dermal neck-joint in *Confractamnis* n.gen. is a very strongly developed projection from the anterior margin of the ADL (cd, Figs. 2, 3). In mesial view, the condyle shows a triangular cross-section. The ventral side of the triangle, with typical "siebknochen" texture of spongy bone (invested with articular cartilage in life), is partly visible in internal view (vs.cd, Fig. 3A). The posterior side of the triangle forms the smooth inner surface, which is slightly convex about a low ridge crossing the condyle from near the mesial termination to the thickened part of the ADL (ri.cd). An anterior view of the ADL plate (Fig. 3B) shows the strong dorsal support for the condyle (the "condylus ridge" of Heintz, 1934: 73), and the mesial termination of the condyle as a rounded point, with its anterodorsal surface (anterior side of triangle) being flat to slightly concave, and also with "siebknochen" texture (sieve-like bone). The actual articular surface is higher laterally than mesially (see Fig. 5C), a condition also noted in both *Dunkleosteus* and *Homostius* by Heintz (1934: 73). Lelièvre (1995) used this as a character to group some primitive brachythoracids from Morocco. Beneath the condyle is a prominent subglenoid process

(pr.sg), which would have articulated against the para-articular process of the skull roof.

The inner surface of the ADL plate shows extensive posterior contact faces for the PDL and PL plates (cf.PDL, cf.PL, Fig. 3A). The distinct anterior margin of the very extensive PDL contact face is marked by vascular grooves (vg) with radiating orientation from the ossification centre of the bone (situated anteriorly in the region of the articular condyle attachment). Ventrally this margin becomes the anterior margin for the PL contact face. A fainter ridge near the posterior border of the ADL plate (ri.p) represents the anterior margin for the more dorsal part of the PL contact face. The anterior half of the inner ADL surface is convex, where the bone is massively thickened (th) to form a broad dorsoventral ridge, decreasing ventrally where the internal convexity lies beneath the deeply incised overlap for the AL plate on the external surface. The posterior part of the inner surface in ANU V1028 is flat to concave, and inflected dorsoventrally at an angle of about 140° about the dorsolateral ridge, at the level of the sensory groove on the external surface. The PDL plate has a similar inflection ("dla" arrow, Fig. 2B).

Associated left PDL and PL plates of *Confractamnis* n.gen. are also partly preserved in the holotype. They can be placed against the ADL plate to confirm their life position. The PDL (Fig. 2B) is missing much of its dorsal part, which was overlapped by the MD plate. Only a narrow posterior strip of the external bone surface is preserved, and most of the bone comprises an internal lamina overlapped extensively by both ADL and PL plates. A thin vertical ridge (ri.vt), which was entirely internal, separates the two overlaps (oa.ADL, oa.PL). The edges of the bone are extremely thin, with many fine fractures which collapsed during acid preparation, and could be only partly reconstructed from fragments. The margins of the bone, however, are indicated by the extent of the contact face inside the ADL plate (cf.PDL, Fig. 3A), which shows that the degree of overlap was more extensive than in many other brachythoracids. The external surface of the PDL plate may have expanded dorsally (PDL, Fig. 4A), and presumably was crossed by a posterior continuation of the lateral line groove (llc). Its distinctive shape can be inferred from the marked dorsoventral elongation of the internal ridge (ri.vt, Fig. 2B), and the extensive overlap surfaces (o.PDL, Fig. 4A). The narrow dorsal corner of the PL plate is still attached to the PDL (PL, Fig. 2B). There is no sign of the internal fossa which received this corner in *Dunkleosteus* (fo.PL, Fig. 6B).

The inner surface of the PDL plate is smooth and concave, inflected about the dorsolateral angle at a level that corresponds to that on the ADL (dla, Fig. 2B). The bone margins show inner vascular grooves like those on the inside of the ADL (vg, Fig. 3A), which may indicate increased blood supply adjacent to the bone margins during periods of growth. The PDL fits inside the ADL such that the vertical ridge (ri.vt, Fig. 2B) abuts against a slight ridge inside the posterior margin of the ADL plate (ri.p, Fig. 3A).

The incomplete PL plate of *Confractamnis* n.gen. (Fig. 2C) is a remarkably high and narrow splint of bone, comprising an anterior overlap area, and high and narrow posterior exposed part. The posterior margin of the preserved part is partly broken, but the form of the inner surface shows that not much is missing. The PL plate slots into the grooved overlap behind the vertical ridge on the PDL (where part of

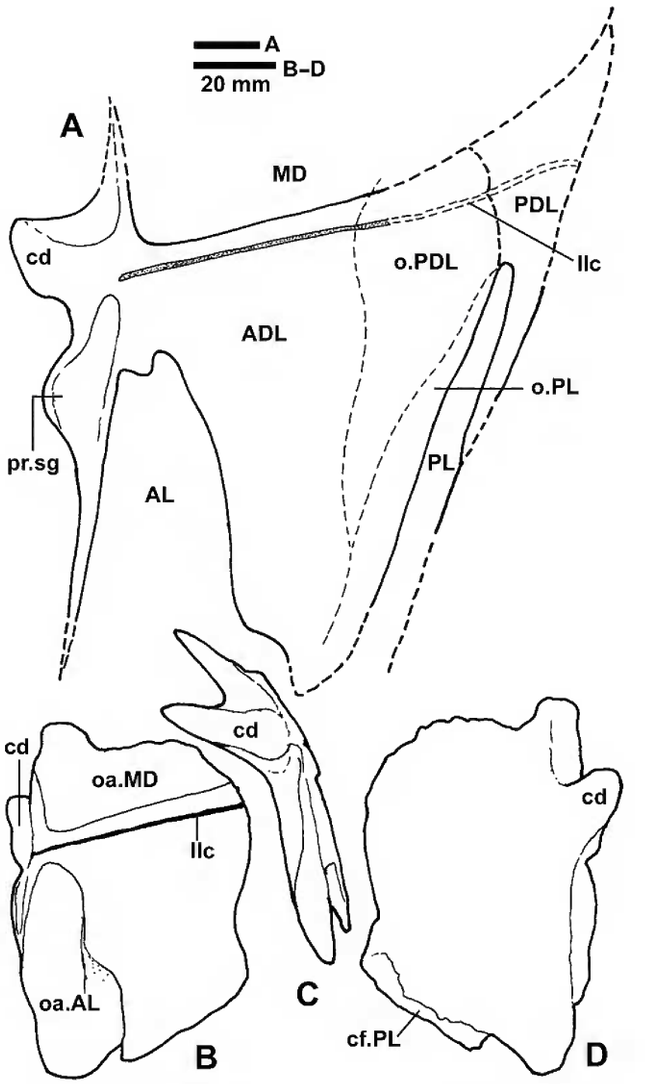

Fig. 4. (*A*) *Confractamnis johnjelli* n.gen. and n.sp. Reconstruction of left lateral side of the trunk armour, based on ANU V1028 (holotype). (*B–D*) Isolated left ADL plate from the Early Devonian of Morocco, in external (*B*), anterior (*C*), and internal (*D*) views. Specimen MCD 62, figured by Lelièvre (1984b: pl. 6F–H).

the PL is still attached; oa.PL, Fig. 2B). With both bones in place inside the ADL, the convex internal surface of the PL forms a thickened posterior border to the articulated armour. Its overlap area is sandwiched between the PDL and ADL plates, with its anterior edge against the posterior ridge dorsally (ri.p, Fig. 3A), and ventrally extending past the PDL to fit into a more deeply incised contact face (cf.PL). This arrangement is summarized in Fig. 4A. The ventral part of the PL plate is unknown.

One small fragment of the AL plate is also preserved attached to the external surface of the ADL in ANU V1028. Otherwise this bone is unknown, except for the distinctive shape of its dorsal part (AL, Fig. 4A), as indicated by the overlap area on the ADL.

The only other arthrodire specimen from locality UQL 4399 also belonged to a brachythoracid, and is provisionally referred to *Confractamnis* n.gen. ANU V1031 is an incomplete MD plate that lacks most diagnostic characters. However the external surface is largely smooth, with similar texture to the small portion of MD attached to the ADL plate in ANU V1028, which is consistent with it belonging to a smaller individual of the same taxon. The more complete

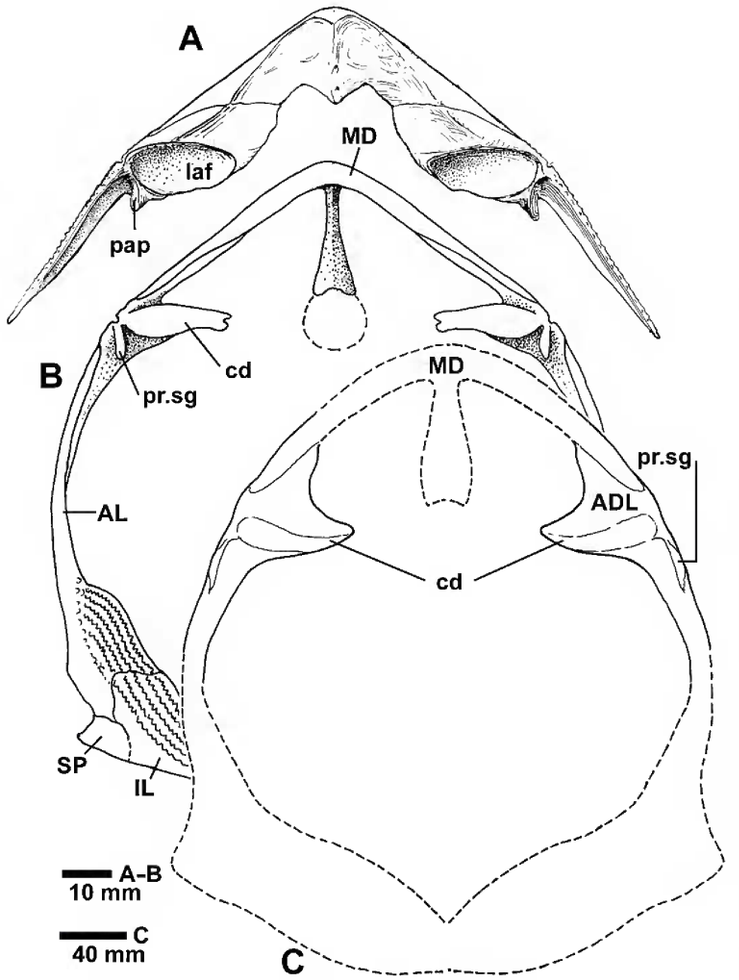

Fig. 5. Brachythoracid trunk armour restorations. (*A,B*) *Taemasosteus* (Early Devonian, Burrinjuck, NSW). (*A*) Posterior view of skull (from White, 1978: fig. 79); (*B*) anterior view of trunk armour, restored from individual bones, using *Harrytoombsia* as a model, as illustrated by Miles & Dennis (1979: fig. 9). (*C*) *Confractamnis johnjelli* n.gen. and n.sp.; trunk armour restoration, anterior view, based on *Taemasosteus* and *Harrytoombsia*.

left lamina is gently curved, 95 mm from the midline to the preserved lateral edge, and 50 mm across between broken anterior and posterior margins. As all margins are incomplete, and no contact faces for the ADL and PDL plates can be discerned on the internal surface, there is insufficient information for a reasonable estimate of total length and overall shape. The bone may have been slightly broader than long, consistent with the shape of the MD overlap area on the ADL plate of the holotype (MD, Fig. 4A). This suggests a somewhat angular shape, and a straight to gently curved lateral margin.

The MD plate of ANU V1031 evidently came from an individual only about half the size of the holotype, but the bone reaches about 10 mm thickness close to the midline. The incomplete carinal process is 70 mm long and 50 mm deep as preserved. Its anteroventral edge thins to about 1 mm, and probably not much is missing. The posteroventral edge is expanded to a thickness of about 8 mm, but is incomplete in lacking the knob-like or grooved termination that is normally developed on the carinal process. The angle between the carinal process and the left lamina is about 75°.

Reconstruction

Arriving at a reliable three-dimensional reconstruction of the trunk armour of a brachythoracid from isolated bones is difficult. It took over 120 years from the first attempts (Miller, 1841) for a reliable reconstruction of the armour of *Coccosteus* (Miles & Westoll, 1968: fig. 44), this reconstruction depending on earlier attempts for other forms (e.g., *Dunkleosteus* Heintz, 1932: fig. 68; *Homostius* Heintz, 1934: fig. 45).

With the discovery of exceptional three-dimensional preservation in the acid-prepared arthrodires from Gogo, Western Australia, it was possible to check the reliability of such restorations with actual specimens. Trial and error in the Natural History Museum, London, showed that if bones were glued together with a tight fit on the clearly defined overlap areas, the left and right sides did not join up—only by leaving a small space around the edges of bone overlaps could a symmetric reconstruction be achieved (Dr R.S. Miles, pers. comm.). The first illustration of an actual reconstructed specimen from the uniquely preserved Gogo fauna was the holotype of *Harrytoombsia* by Miles & Dennis (1979: fig. 9).

The ADL plate on its own is one of the most informative in attempting a reconstruction from isolated bones, because the axis of articulation on the condyle must have been horizontal for the dermal neck-joint to function in the living animal. This provides some constraint on the cross-sectional shape of the trunk armour, a point first exploited by Heintz (1934: fig. 47) in comparing *Dunkleosteus* with the dorsoventrally compressed armour of *Homostius*. There is, however, always a degree of uncertainty regarding the precise orientation of the axis of articulation, because the condyle in life was invested with articular cartilage, so its true shape is not preserved. Thus, it is possible that the ADL may have been slightly more steeply inclined (implying a higher trunk armour) than depicted in the reconstruction (Fig. 5C), although the preserved angles of the MD plate in ANU V1031 are generally consistent with this reconstruction.

Using the trunk armour in the holotype of *Harrytoombsia* as a model (Miles & Dennis, 1979: fig. 9), the armour of *Confractamnis* n.gen. may have been some 37 cm in height, and over 30 cm across. As there is no control of the width across the articular condyles of the ADL, the armour could have been considerably larger by comparison with *Harrytoombsia* (which has proportionately smaller condyles), but it is unlikely to have been any smaller. Such a fish would have been at least 206 cm long, judging by proportions in *Coccosteus cuspidatus*, where whole animals including the tail are preserved, and total length of the fish is some 5.5 times trunk armour height (see Miles & Westoll, 1968: figs. 44, 48).

Discussion

The trunk armour bones of *Confractamnis* n.gen. just described reveal many characters by which they can be distinguished from other arthrodires. On the ADL plate, the groove for the main lateral line sensory canal (llc, Fig. 4A) crosses the bone close and subparallel to the edge of the overlap for the MD, which is a point of difference to many other brachythoracids. In *Coccosteus* and *Harrytoombsia* (Miles & Westoll, 1968: fig. 30; Miles & Dennis, 1979: fig. 4) there are two branches, the main one passing postero-ventrally across the ADL plate. In *Dunkleosteus* and

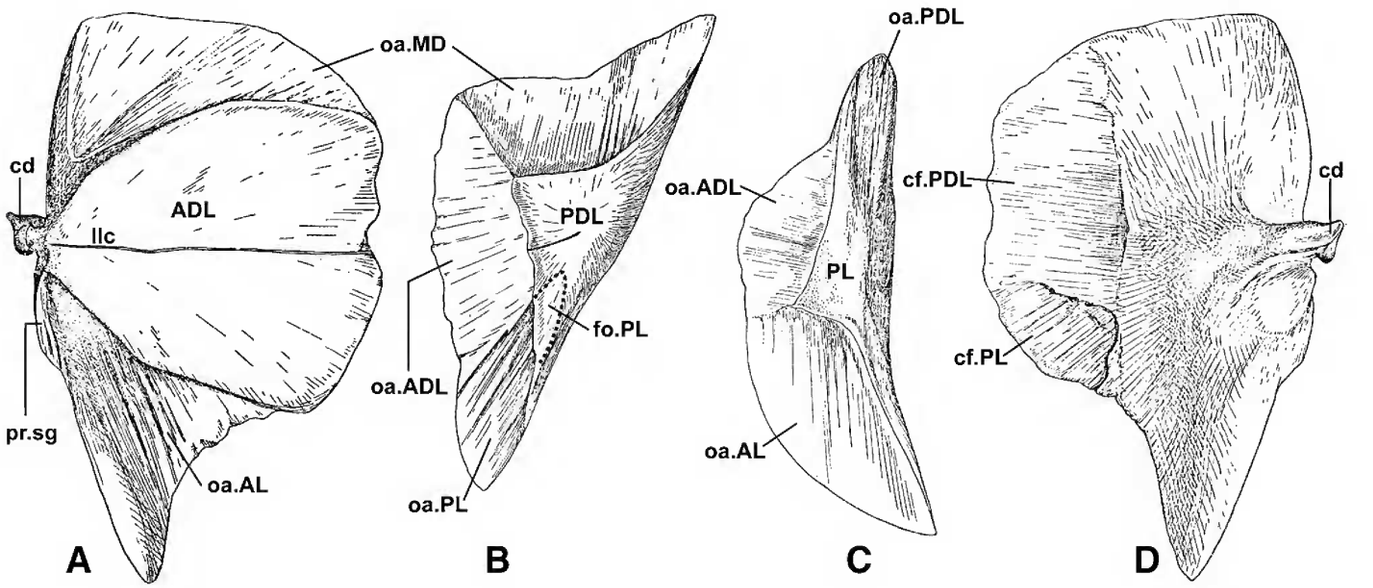

Fig. 6. Left trunk armour bones of the Late Devonian brachythoracid *Dunkleosteus*, arranged to show overlap relations (not to scale). (*A,D*) ADL plate in lateral and internal views (reversed images from Heintz, 1932: figs. 46–n>47); (*B*) PDL plate, and (*C*) PL plate, both in external view (from Heintz, 1932: figs. 49, 54).

Eastmanosteus (Heintz, 1932: fig. 46; Dennis-Bryan, 1987: fig. 22A), there is some distance between the groove and the MD overlap, with similar exposed areas of the ADL plate both above and below the groove (Fig. 6A). In *Holonema*, the arrangement is different again, with the straight sensory groove crossing the ADL close to and subparallel with the ventral overlap for the AL plate (Miles, 1971: figs. 62, 63).

The forms most similar to *Confractamnis* n.gen. in the position of the sensory groove are *Taemasosteus* and *Tityosteus* from the Early Devonian (White, 1978: fig. 102; Gross, 1960: fig. 1B), in which it passes straight back from the level of the condyle, running subparallel to the edge of the MD overlap. However the ADL plate in both of these taxa has a triangular ventral overlap area for the AL plate, of similar shape to that of *Dunkleosteus* (Fig. 6A). The large Middle Devonian brachythoracid *Heterostius* also has a dorsally placed sensory groove on the ADL (Denison, 1978: fig. 48B), but in this case the AL plate is reduced to a massive splint of bone fused to the ADL, a unique specialization of this family. The prominently projecting articular condyle in ANU V1028 shows that *Confractamnis* n.gen. could not have had a dorsoventrally compressed armour, thus excluding a close relationship with *Atlantidosteus*, another large arthrodire documented from both Morocco and the Broken River Sequence, and referred to the Homostiidae (Lelièvre, 1984a; Young, 2003a).

Two examples of the ADL plate from the late Emsian of Morocco resemble *Confractamnis* n.gen. in the unusual shape of the AL overlap area. In the holotype of *Antineosteus*, the ADL has a sensory groove that is more ventrally placed with respect to the MD overlap (Lelièvre, 1984b: fig. 16A). The articular condyle in this form is developed completely differently, with an elongate attachment to the front margin of the bone indicating a depressed body form typical of the family Homostiidae. Another left ADL (MCD 62), from the same locality (near Akka), was figured without further comment as "Homostiid sp." by Lelièvre (1984b, pl. 6F–H). It is closely similar to ANU V1028 in the highly angular overlap for the AL, and the orientation of the sensory groove, which has a straight course, running close to and subparallel with the ventral edge of the overlap for the MD plate (Fig. 4B). This taxon is clearly not conspecific with *Confractamnis* n.gen., since the specimen has much coarser tuberculate ornament, even though it is only about half the size of the ADL plate in the holotype. It also probably differs in having the exposed ornamented part extending ventrally past the edge of the AL overlap (but the corresponding margin is broken in ANU V1028). The articular condyle in the Moroccan specimen (cd, Fig. 4B–D) has a similar pointed mesial end in anterior view to *Confractamnis* n.gen., but is more elongate.

The thickened dorsal attachment of the condyle to the main body of the ADL plate in *Confractamnis* is quite different to that of *Taemasosteus* (Fig. 5), and a range of other brachythoracids where this has been illustrated (e.g., Heintz, 1932: fig. 68, 1934: fig. 45; Lelièvre *et al.*, 1981: figs. 7, 15). The thickenings on the inner surface of the ADL in *Confractamnis* (Fig. 3A) are similarly developed to a much smaller ADL plate belonging to the homostiid *Cavanosteus* from Burrinjuck (Young, 2004c: fig. 6), but it is not clear if this is a general or primitive brachythoracid feature.

The PDL plate of *Confractamnis* n.gen., although incompletely preserved, also demonstrates a distinctive morphology compared to other brachythoracids. Its margins, as indicated by the extent of the contact face inside the ADL, show that the degree of overlap was much more extensive than in forms like *Taemasosteus, Antineosteus* or *Heintzichthys* (White, 1978: fig. 105; Lelièvre, 1984b: fig. 16B; Carr, 1991: fig. 6B). *Heintzichthys, Coccosteus* and *Eastmanosteus* have a typical brachythoracid PDL plate of approximately equilateral triangular shape, with three overlap surfaces, essentially as in *Dunkleosteus* (Fig. 6B). An internal fossa for the dorsal corner of the PL plate (fo.PL) was interpreted by Carr (1991: 383) as one of five characters uniting *Eastmanosteus* and *Dunkleosteus* in the family Dinichthyidae, but this is absent in all Emsian-Eifelian brachythoracid taxa known so far.

Only the dorsal part of the PL plate is preserved in *Confractamnis* n.gen., but again it indicates a distinctive

shape. In most other brachythoracids this bone has more equilateral proportions, but with similar overlap relations to surrounding bones. In *Heintzichthys* for example (Carr, 1991: fig. 10), the PL plate overlaps the PDL, and the ADL plate overlaps its anterodorsal part, which is sandwiched between the ADL on the outside, and the overlap surface of the PDL on the inside, essentially as in *Dunkleosteus* (Fig. 5C). Brachythoracids typically show a similar connection dorsally with the PDL plate, which carries a narrow dorsal notch to receive the dorsal angle of the PL, in *Eastmanosteus* and *Dunkleosteus* developed as a fossa (fo.PL, Fig. 6B). In *Antineosteus* the PL is only known from a small narrow dorsal part in the type specimen (H. Lelièvre, pers. comm.), and from its contact face on the PDL plate, which shows a narrow dorsal notch. It is clear that the overlapped area of ANU V1028 was much more extensive, indicating that the PL plate of *Confractamnis* n.gen. was much higher and narrower than in *Antineosteus*. In *Taemasosteus*, as restored by White (1978: figs. 103–105), the PL plate overlaps the PDL, but sits entirely behind, and is not overlapped by, the ADL plate. It therefore has only one ventral overlap area, for the AL plate.

In some derived brachythoracids the PL plate may be much reduced, or completely lost. This was assumed to be the case for *Homostius* by Heintz (1934), until it was recorded (with a SP plate, also assumed to be missing in this taxon) from a new Estonian locality (Karski). The PL of *Homostius*, as described by Mark-Kurik (1993), resembles that of *Confractamnis* n.gen. in its high and narrow shape, but differs in the fact that the external part expands rather than narrows dorsally. It also carries a sensory groove, even though the normal condition in brachythoracids is for the sensory groove to cross the ADL and PDL plates. A shift in the position of the sensory canal may relate to the broad, dorsoventrally compressed body form of *Homostius* (Heintz, 1934: fig. 49).

The MD plate in *Confractamnis* n.gen. is interpreted, mainly from its overlap on the ADL plate of the holotype, to have been slightly broader than long, somewhat angular in shape, and with a straight to gently curved lateral margin. Several other brachythoracids have similar MD plates, including *Homostius* and *Antineosteus* (Heintz, 1934; Lelièvre, 1984b). In *Dunkleosteus, Taemasosteus* and *Tityosteus* the MD plate has a more elongate and rounded lateral profile (Heintz, 1932: fig. 44; White, 1978: fig. 94; Otto, 1992: fig. 6a). The 75° angle between the carinal process and the left lamina is less arched than in *Taemasosteus* (about 50°; White, 1978: fig. 95), but not as flat as in *Homostius* or *Tityosteus* (e.g., Heintz, 1934; Gross, 1960). Krasnov & Mark-Kurik (1982) identified an isolated MD plate from the Emsian of the Minusinsk area of Russia as a new species *Tityosteus orientalis*. This was also less arched than in *Confractamnis* n.gen., with an angle of about 60° between the carinal process and one lamina of the MD.

The attempted reconstruction of the trunk armour of *Confractamnis* n.gen. (Fig. 5C) can be compared with a similar reconstruction of the Emsian form *Taemasosteus* from Burrinjuck, where additional information from the skull roof (White, 1978: fig. 79) provides a constraint on the width between the articular condyles (Fig. 5A–B). Both these taxa may have had bodies with an overall fusiform shape, in contrast to the dorsoventrally compressed shape of *Homostius* and related taxa. However it is possible that relative height of the neck-joint articulation varied, and was carried higher on the armour in *Coccosteus* or *Harrytoombsia*, which may be the reason that the main sensory groove across the external surface of the ADL plate has a characteristic downward course in these taxa, presumably to align with the middle part of the flank as it ran back onto the tail of the fish (cf. Miles, 1971: fig. 108).

Conclusions and summary

The new taxon *Confractamnis* n.gen., from assumed Eifelian strata in the Broken River sequence of Queensland, shows closest affinity amongst known forms to some arthrodire material from the late Emsian of Morocco. This suggests the same distribution pattern as that indicated for the homostiid arthrodire *Atlantidosteus*, represented by two species with a disjunct distribution in the Devonian of Morocco and Queensland (Young, 2003a). Faunal connections, and continuity of shallow tropical to subtropical marine environments along the eastern and northern margins of the Gondwana supercontinent, are indicated by this pattern. On most current reconstructions the northern Gondwana margin had a palaeolatitude between 0–30°S (e.g., Young, 2003b: fig. 2). The only other likely connection (constrained by palaeolatitude) would be across the proto-Pacific Ocean, assuming this large ocean existed in the early-middle Palaeozoic (cf. Nur & Ben-Avraham, 1981). An alternative proposal, based on the evidence of Devonian fish distributions, is that palaeogeographic change during the middle Palaeozoic involved increasing proximity between Gondwana and Laurussia (Euramerica), with first shallow marine, and then non-marine fish dispersal between the two continental blocks during the Middle and Late Devonian (Young *et al.*, 2000a,b; Young & Moody, 2002; Young, 2003b).

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References

Carr, R.K., 1991. Reanalysis of *Heintzichthys gouldii* (Newberry), an aspinothoracid arthrodire (Placodermi) from the Famennian of northern Ohio, with a review of brachythoracid systematics. *Zoological Journal of the Linnean Society* 103: 349–390.

Carr, R.K., 1995. Placoderm diversity and evolution. *Bulletin du Muséum national d'Histoire naturelle, Paris, Section C*, 17: 85–125.

De Pomeroy, A.M., 1995. Australian Devonian fish biostratigraphy in relation to conodont zonation. *Courier Forschungsinstitut Senckenberg* 182: 475–486.

De Pomeroy, A.M., 1996. Biostratigraphy of Early and Middle Devonian microvertebrates from Broken River, north Queensland. *Records of the Western Australian Museum* 17: 417–437.

Denison, R.H., 1978. Placodermi. In *Handbook of Paleoichthyology*, ed. H.-P. Schultze, vol 2. Stuttgart, New York: Gustav Fischer Verlag, 128 pp.

Denison, R.H., 1984. Further consideration of the phylogeny and classification of the Order Arthrodira (Pisces: Placodermi). *Journal of Vertebrate Paleontology* 4: 396–412.

Dennis-Bryan, K.D., 1987. A new species of eastmanosteid arthrodire (Pisces: Placodermi) from Gogo, Western Australia. *Zoological Journal of the Linnean Society* 90: 1–64.

Goujet, D., & G.C. Young, 1995. Interrelationships of placoderms revisited. *Geobios, Memoire special* 19: 89–96.

Gross, W., 1932. Die Arthrodira Wildungens. *Geologische u. Paläontologische Abhandlungen* 19: 5–61.

Gross, W., 1960. *Tityosteus* n.gen. ein Reisenarthrodire aus dem rheinischen Unterdevon. *Paläontologische Zeitschrift* 34: 263–274.

Heintz, A., 1932. The structure of *Dinichthys*: a contribution to our knowledge of the Arthrodira. *Bashford Dean Memorial Volume-Archaic Fishes* 4: 115–224.

Heintz, A., 1934. Revision of the Estonian Arthrodira. Part I. Family Homostiidae Jaekel. *Publications of the Geological Institution of the University of Tartu*, no. 38. Tartu, 114 pp.

Krasnov, V.I., & E. Mark-Kurik, 1982. The first find of fossil fish in the limestones of the Tashtyp Formation of the south Minusinsk Depression. *Transactions of the Institute of Geology and Geophysics, Siberian Branch, USSR Academy of Sciences* 483: 47–52.

Lelièvre, H., 1984a. *Atlantidosteus hollardi* n.g., n.sp., nouveau Brachythoraci (vertébrés, placodermes) du Dévonien inférieur du Maroc présaharien. *Bulletin du Muséum national d'Histoire naturelle, Paris* 6: 197–208.

Lelièvre, H., 1984b. *Antineosteus lehmani* n.g., n.sp., nouveau Brachythoraci du Dévonien inférieur du Maroc présaharien. Remarques sur la paléobiogéographie des homostéides de l'Emsien. *Annales de Paléontologie* 70: 115–158.

Lelièvre, H., 1995. Description of *Maideria falipoui* n.g., n.sp., a long snouted brachythoracid (Vertebrata, Placodermi, Arthrodira) from the Givetian of Maider (South Morocco), with a phylogenetic analysis of primitive brachythoracids. *Bulletin du Muséum national d'Histoire naturelle, Paris* 17: 163–207.

Lelièvre, H., P. Janvier & D. Goujet, 1981. Les vertébrés Dévonien de l'Iran central: IV, arthrodires et ptyctodontes. *Géobios* 14: 677–709.

Mark-Kurik, E., 1993. Remarks on the trunk-shield structure in *Homostius* (Placodermi). *Proceedings of the Estonian Academy of Sciences. Geology* 42: 176–180.

Mark-Kurik, E., & G.C. Young, 2003. A new buchanosteid arthrodire (placoderm fish) from the Early Devonian of the Ural Mountains. *Journal of Vertebrate Paleontology* 23: 13–27.

Mawson, R., & J.A. Talent, 1989. Late Emsian-Givetian stratigraphy and conodont biofacies—carbonate slope and offshore shoal to sheltered lagoon and nearshore carbonate ramp—Broken River, north Queensland, Australia. *Courier Forschungsinstitut Senckenberg* 117: 205–259.

McCoy, F., 1848. On some new fossil fishes of the Carboniferous period. *Annals and Magazine of Natural History* 2: 1–10.

Miles, R.S., 1971. The Holonematidae (placoderm fishes), a review based on new specimens of *Holonema* from the Upper Devonian of Western Australia. *Philosophical Transactions of the Royal Society of London. B. Biological Sciences* 263: 101–234.

Miles, R.S., & K. Dennis, 1979. A primitive eubrachythoracid arthrodire from Gogo, Western Australia. *Zoological Journal of the Linnean Society* 66: 31–62.

Miles, R.S., & T.S. Westoll, 1968. The placoderm fish *Coccosteus cuspidatus* Miller ex Agassiz from the Middle Old Red Sandstone of Scotland. Part I. Descriptive morphology. *Transactions of the Royal Society of Edinburgh* 67: 373–476.

Miller, H., 1841. *The Old Red Sandstone*. Edinburgh: Johnstone and Hunter.

Nur, A., & Z. Ben-Avraham, 1981. Lost Pacifica continent: a mobilistic speculation. In *Vicariance Biogeography: A Critique*, ed. G. Nelson & D.E. Rosen, pp. 341–358. New York: Columbia University Press, 593 pp.

Otto, M., 1992. Ein Neufund des brachythoracen Arthrodiren *Tityosteus rieversi* aus dem unterdevonischen Hunsrückschiefer des rheinischen Schiefergebirges. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 187: 53–82.

Otto, M., 1999. New finds of vertebrates in the Middle Devonian Brandenberg Group (Sauerland, Northwest Germany). *Paläontologische Zeitschrift* 72: 117–134.

Sloan, T.R., J.A. Talent, R. Mawson, A.J. Simpson, G.A. Brock, M.J. Engelbretsen, J.S. Jell, A.K. Aung, C. Pfaffenritter, J. Trotter & I.W. Withnall, 1995. Conodont data from Silurian-Middle Devonian carbonate fans, debris flows, allochthonous blocks and adjacent autochthonous platform margins: Broken River and Camel Creek areas, north Queensland, Australia. *Courier Forschungsinstitut Senckenberg* 182: 1–77.

Turner, S., A. Basden & C.J. Burrow, 2000. Devonian vertebrates of Queensland. In *IGCP 328, Final Report*, ed. A. Blieck & S. Turner. *Courier Forschungsinstitut Senckenberg* 223: 487–521.

Turner, S., & A. Cook, 1997. Ptyctodont jaw from the Broken River Province, NEQ. *Memoirs of the Queensland Museum* 42: 80.

White, E.I., 1978. The larger arthrodiran fishes from the area of the Burrinjuck Dam, N.S.W. *Transactions of the Zoological Society of London* 34: 149–262.

Woodward, A.S., 1891. *Catalogue of Fossil Fishes. Part 2*. London: British Museum (Natural History), 567 pp.

Young, G.C., 1986. The relationships of placoderm fishes. *Zoological Journal of the Linnean Society* 88: 1–57.

Young, G.C., 1990. New antiarchs (Devonian placoderm fishes) from Queensland, with comments on placoderm phylogeny and biogeography. *Memoirs of the Queensland Museum* 28: 35–50.

Young, G.C., 1993. Middle Palaeozoic macrovertebrate biostratigraphy of Eastern Gondwana. In *Palaeozoic Vertebrate Biostratigraphy and Biogeography*, ed. J.A. Long, pp. 208–251. London: Belhaven Press, 369 pp.

Young, G.C., 1996. Devonian (chart 4). In *An Australian Phanerozoic Timescale*, ed. G.C. Young, & J.R. Laurie, pp. 96–109. Melbourne: Oxford University Press, 279 pp.

Young, G.C., 2003a. A new species of *Atlantidosteus* Lelièvre, 1984 (Placodermi, Arthrodira, Brachythoraci) from the Middle Devonian of the Broken River area (Queensland, Australia). *Geodiversitas* 25: 681–694.

Young, G.C., 2003b. North Gondwanan mid-Palaeozoic connections with Euramerica and Asia; Devonian vertebrate evidence. *Courier Forschungsinstitut Senckenberg* 242: 169–185.

Young, G.C., 2003c. Did placoderm fish have teeth? *Journal of Vertebrate Paleontology* 23: 987–990.

Young, G.C., 2004a. Large brachythoracid arthrodires (placoderm fishes) from the Early Devonian of Wee Jasper, New South Wales, Australia. *Journal of Vertebrate Paleontology* 24: 1–17.

Young, G.C., 2004b. A Devonian brachythoracid arthrodire skull (placoderm fish) from the Broken River area, Queensland. *Proceedings of the Linnean Society of New South Wales* 125: 43–46.

Young, G.C., 2004c. A homostiid arthrodire (placoderm fish) from the Early Devonian of the Burrinjuck area, New South Wales. *Alcheringa* 28: 129–146.

Young, G.C., & J.M. Moody, 2002. A Middle-Late Devonian fish fauna from the Sierra de Perijá, western Venezuela, South America. *Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe* 5: 153–204.

Young, G.C., H. Lelièvre & D. Goujet, 2001. Primitive jaw structure in an articulated brachythoracid arthrodire (placoderm fish; Early Devonian) from southeastern Australia. *Journal of Vertebrate Paleontology* 21: 670–678.

Young, G.C., J.A. Long & C. Burrow, 2000a. Devonian vertebrates, In *Palaeobiogeography of Australasian Faunas and Floras*, ed. A.J. Wright, G.C Young, J.A. Talent & J.R. Laurie, *Association of Australasian Palaeontologists, Memoir* 23: 209–218.

Young, G.C., J.A. Long & S. Turner, 1993. Faunal lists of Eastern Gondwana Devonian macrovertebrate assemblages. In *Palaeozoic Vertebrate Biostratigraphy and Biogeography*, ed. J.A. Long, pp. 246–251. London: Belhaven Press, 369 pp.

Young, G.C., J. Moody & J. Casas, 2000b. New discoveries of Devonian vertebrates from South America, and implications for Gondwana-Euramerica contact. *Comptes Rendus de l'Academie des Sciences, Paris*, 331: 755–761.

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